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ABSTRACT

Land preservation and restoration are important tools for managing imperiled aquatic species, but they are often applied in the absence of a transparent scheme of geographic prioritization. To help guide preservation and restoration efforts in the Conasauga River Basin in Georgia and Tennessee, we used the "Zonation" algorithm to prioritize sub-watersheds. Zonation is a prioritization system that uses species occurrence to identify localities of highest biodiversity, greatest interconnectivity, and (optionally) lowest cost. We based the prioritization on known and predicted distributions of 10 imperiled fish species and 12 imperiled invertebrate species, with predicted distributions derived from maximum entropy niche modeling. In the resulting prioritization scheme, highly ranked areas included the Conasauga River mainstem, the Conasauga headwaters, and the Holly Creek tributary system. We propose that a prioritization such as this should be conducted prior to any major program of land preservation or restoration.

INTRODUCTION

Protected reserves are often regarded as the backbone of species-oriented conservation (Margules and Pressey, 2000). Although the reserve approach *per se* has not been widely applied in freshwater biodiversity management (Abell et al., 2007), governments have been buying and protecting land for the enhancement of game species for centuries, sometimes to the benefit of other fishes and invertebrates. In many locations, freshwater biodiversity also benefits inadvertently from the protection of mountainous, forested headwaters. To date, however, many such preservation efforts have been opportunistic and have not been guided by an overarching plan that considers the distributions and needs of imperiled species. In contrast to freshwater reserves, freshwater "restoration" measures have received extensive attention and are far more controversial (Simon et al., 2007). Here we define restoration to mean direct modification of stream channels with the goal of enhancing some aspect of stream function or structure. This has emerged as a billion dollar a year industry, but there continues to be considerable debate as to whether many restoration projects achieve ecological or social benefits, or whether they do so in a cost-effective manner (Bernhardt et al., 2005; Palmer et al., 2005). There have been numerous restoration projects conducted in the Southeast, including in the Upper Coosa Basin, but like preservation efforts their locations have rarely been selected through a transparent prioritization scheme (Sudduth et al., 2007). Rather, many sites have been selected on the basis of land availability, usually without consideration of a larger watershed plan (Sudduth et al., 2007). Benefits to imperiled aquatic species are usually considered only secondarily.

Because both land preservation and stream restoration are expensive tools, there is a general public interest in ensuring that they are employed in a way that maximizes the benefit-cost ratio and, in particular, that they are applied in the appropriate geographic locations (Sarkar et al., 2006). This requires a method for prioritizing or ranking localities. A key element of conservation prioritization is irreplaceability: the identification of locations that are essential for supporting the full biodiversity of the area (Margules and Pressey, 2000; Brooks et al., 2006; Sarkar et al., 2006). Numerous algorithms have been developed to determine optimal locations (Sarkar et al., 2006), but most of these methods can be divided into two broad categories: scoring procedures and complementarity-based algorithms (Abellan et al., 2005). Scoring procedures rank all potential locations on the basis of criteria such as species richness, vulnerability, and rarity, then select the highest ranking areas. Complementarity methods consider the additional benefit of each potential location when added to existing or potential protected areas. These algorithms outperformed scoring procedures in efficiently identifying a network of reserve sites for biodiversity (Abellan et al., 2005). One well-developed example of a complementarity algorithm is the "Zonation" method (Moilanen et al., 2005; Moilanen, 2007), which was created for terrestrial systems but has been recently extended to cover freshwater applications (Moilanen et al., 2008).

The objective of this study was to use the Zonation algorithm to prioritize sub-watersheds (USGS HUC-12 level) of the Conasauga River sub-basin, part of the Upper Coosa system in North Georgia and Southeast Tennessee. Our goal was to rank sub-watersheds according to their importance in preserving the imperiled aquatic biodiversity of the river system, defined here as federally or state protected vertebrates and invertebrates (Tables 1 and 2). This will help to guide both preservation and restoration efforts to those sub-watersheds of the Conasauga where they may provide the greatest benefit.

STUDY AREA AND SPECIES

The Conasauga River is a tributary of the Coosa in the Mobile drainage, located in the Blue Ridge and Valley and Ridge physiographic provinces of Northwest Georgia and Southeast Tennessee. It is a highly diverse river system with approximately 77 extant native fish species, 15 introduced fish species, and six fish species presumed to be extirpated (Walters, 1997). Although most of its fish fauna is intact, only 19 of the 37 historically present mussel species are believed to persist (Novak et al., 2004). Those mussel species that remain may be threatened by high nutrient concentrations and toxic contaminants in sediments originating from agricultural activities (Sharpe and Nichols, 2007). Ten of the fish species (Table 1) and 14 of the mussel species (Table 2) are listed as threatened or endangered by the state of Georgia and/or by the U.S. Fish and Wildlife Service. These 24 species are the focus of this study.

METHODS

We used the software Zonation 2.0 (Moilanen, 2008) to prioritize sub-watersheds. Zonation is a prioritization system that uses species occurrence to identify localities of highest biodiversity, greatest interconnectivity, and (optionally) lowest cost. Zonation implements an algorithm that starts with the full landscape of interest and iteratively discards locations (cells) of lowest value in terms of species occurrence and connectivity (Moilanen et al., 2005; Moilanen, 2007). The result is a nested hierarchy of solutions that seek to maximize coverage of species habitat and connectivity for any given number of cells. Zonation 2.0 includes options specifically designed for freshwater conservation that allow for watershed-based analysis and upstream-downstream connectivity among watersheds (Moilanen et al., 2008). Below we describe the preparation of known and estimated species occurrence data (the latter we term species potential ranges) used in the analysis, followed by an explanation of the Zonation analysis itself.

We drew species occurrence data from a database maintained by the Georgia Museum of Natural History. We considered records between 1995 and 2007 which represent a 13-year time span centered on the year of most recent land cover data (2001). This was important because land cover data were used to estimate species potential ranges, as described in the next section, so we wanted the species data to be roughly contemporaneous with the land cover data. We excluded a small number of species records we considered dubious because they fell well outside the species' known ranges and preserved individuals were unavailable for verification. The full data set included 463 fish collection records and 523 mussel and crayfish collection records. Occurrence data for these collections can be viewed at the online supplement (Supplemental Figures S1-S6; http://ichthyology.usm.edu/sfc/proceedings/supplementary/Wenger_etal.pdf).

Because the species data were originally collected for different purposes, the intensity of sampling effort was not uniform across all sub-watersheds, nor was it consistent across taxa. Prioritization based solely on these recorded locations might produce a biased estimate, emphasizing those sub-watersheds with higher sampling densities and those species with better-defined ranges. In an effort to mitigate this bias, we developed species niche models and used them to predict the probability of species occurrences in sub-watersheds where the species had not been collected (i.e., the species "potential ranges"). For sub-watersheds where little or no sampling has been conducted (these differ for fishes and mussels; Supplemental Figures S1-S6), this prediction represents the probability that a species might actually occur there. For sub-watersheds where significant sampling has occurred, a prediction of presence suggests that factors other than those included in the model (see below) are important in determining species absence. These could include historical land use activities that caused extirpations.

We used maximum entropy modeling (Phillips et al., 2006a) to calculate potential ranges. With this approach, geographic coordinates of species occurrence data are overlain on a set of environmental raster data and maximum likelihood methods are used to identify the distribution closest to uniform (i.e., that of maximum entropy) which satisfies the constraints imposed by the environmental variables. The resulting model is then applied to the landscape. Maximum entropy is not a new technique, but it has recently become popular for species niche modeling because it can be used with presence-only data, it is now supported by a convenient software interface (MaxEnt; Phillips et al., 2006b) and its performance compares well to other niche modeling methods (Elith et al., 2006). Our data set did include absence data, but collections were made with differing methods and varying degrees of effort, resulting in variable detection probability. As a consequence, the reliability of absence records is difficult to estimate under conventional methods (such as generalized linear modeling) without extensive additional analysis or exclusion of significant portions of the data. In contrast, maximum entropy can make efficient use of this heterogenous data set.

We did not attempt to model species that were recorded only at a few (< 15) separate sites, because such sparse data sets provide little information to define distributions. The excluded species were *Noturus* sp. cf. *munitus* (Coosa madtom), *Etheostoma ditrema* (coldwater darter), *Percina lenticula* (freckled darter), *Cambarus cymatilis* (Conasauga blue burrower), *Elliptio arctata* (delicate spike), *Medionidus acutissimus* (Alabama moccasinshell), *M. parvulus* (Coosa moccasinshell), and *Strophitus subvexus* (southern creekmussel). For the remaining 14 species, we selected five environmental variables as potential predictors: sub-watershed drainage area, elevation, number of dams in the sub-watershed, total impervious area, and forest cover, all of which we had found to be useful predictors of fish occurrence in a previous analysis in the nearby Etowah sub-basin (Wenger et al., 2008). We hypothesized that these five variables explained a significant amount of the variation in species distribution patterns. Sub-watershed drainage area ("area") was calculated by creating an artificial drainage area map from USGS digital elevation models. Elevation was derived from USGS digital elevation models. We calculated dams per sub-watershed ("dams") by (1) identifying dams from reservoirs that appeared on USGS topographic quadrangles and aerial photos and (2) summing the number of dams in each USGS HUC-12 sub-watershed. Total impervious area (TIA) was derived from the 2001 National Land Cover Database Zone 54 Impervious Layer (USGS, 2003). In a previous study we found that the presences and absences of some fish species were well predicted by impervious cover within 1.5 km of the collection site (Wenger et al., 2008). Therefore, we transformed the TIA coverage by replacing the value for each pixel by the mean of a 1.5 km radius circle around it. Forest cover was derived from 2001 land cover data (Kramer, 2004) and transformed in the same manner as the TIA coverage. Each environmental variable was input as a raster with a resolution of 180 m. This low resolution helped to ensure that collection points aligned correctly with streams and rivers in the drainage area coverage.

The MaxEnt program allows various transformations of environmental variables, such as quadratic, product (interactions), and thresholds. We used the "auto features" setting which determined which transformations to allow based on the size of the data set for each species, using a set of empirically-derived rules (Phillips et al., 2006b). For species that occurred at 25 or more sites, we divided the data set randomly into a training set (90% of records) and a test set (the remaining 10%) for calculating model performance. For species with fewer than 25 collection sites, there was no test set and therefore only an estimate of within-sample model performance. Performance was estimated by the area under the curve (AUC) of the receiver-operator characteristic plot, a method not subject to bias due to species prevalence (Manel et al., 2001).

Zonation Analysis

We assigned each HUC-12 sub-watershed the value of 1 for each species recorded to be present within it, indicating 100% probability of presence. We considered a species' potential range to include those sub-watersheds where a species had not been collected, but where the species was predicted to be present with a probability of 10% or greater in each cell along at least one kilometer of stream based on maximum entropy modeling. All such sub-watersheds were assigned a value of 0.25 for the species in question. Essentially, this gives sub-watersheds within a species' potential range a weighting one fourth that of sub-watersheds with a species' actual range. All species were given equal priority.

Zonation allows for different cell removal rules which govern the prioritization algorithm. We used the "additive benefit function" rule, which emphasizes locations that benefit multiple species, in contrast to the "core area" rule, which seeks to find the best locations for each individual species. We also defined upstream-downstream connectivity among sub-watersheds, which allows for the possibility that failure to protect a sub-watershed can have negative impacts on downstream sub-watersheds. Therefore, if a watershed is prioritized highly due to the presence of target species, its tributary sub-watersheds will also receive some prioritization, regardless of the species they support. Finally, we included a cost layer which was allowed to influence the prioritization. The cost layer was based on land cover and imposed a cost of zero on forested cells, 1 on agricultural cells, and a value equivalent to percent impervious cover (i.e., 1-100) for cells with impervious cover of 1% or greater. These costs are in relative terms and do not have a simple translation to dollar values. The reasoning behind the cost layer is that forested land tends to be relatively inexpensive to acquire and preserve and generally requires little restoration. Agricultural land is somewhat more expensive and more likely to require restoration, whereas land that currently supports suburban and urban uses would be far more expensive to acquire and preserve and might require extensive restoration, depending on the degree of urbanization.

RESULTS

The maximum entropy models had good predictive performance, with AUC > 0.96 in all cases. However, this was largely due to the fact that these are aquatic species that only occur in the relatively small subset of landscape cells that fall within streams or rivers. Therefore, any model that includes sub-watershed drainage area has a high nominal predictive ability, since it can easily predict species absence in terrestrial cells. Accordingly, sub-watershed drainage area was by far the most important explanatory variable for each species (Table 3), contributing between 68.6% and 95.8% of the variance explained for each species (a mean of about 90% overall). The number of dams per sub-watershed was the next most important predictor variable, followed by elevation, TIA, and forest cover, respectively (Table 3).

The Zonation analysis gave highest priority to the reaches of the mainstem (Fig. 1). The headwaters were also ranked highly, primarily due to their importance in protecting the downstream mainstem reaches. Mill Creek, flowing into the mainstem from Tennessee, received a moderately high priority (64) and downstream tributaries generally declined in priority in a downstream direction. Another high priority set of sub-watersheds was the Holly Creek system, whose sub-watersheds scored from 59-70 due mainly to a high number of listed mussel species. Tributaries in the Dalton area and tributaries to the lowest reaches of the mainstem ranked the lowest. Most of Coahulla tributary system also ranked low, but the Coahulla mainstem received a moderate priority because maximum entropy modeling showed it to be potential habitat for multiple fish and mussel species, even though it currently supports very few.

DISCUSSION

The prioritization algorithm gave the highest ranking to the Conasauga River mainstem and headwaters, which is reasonable because most of the imperiled species of the sub-basin can be found within these sub-watersheds. The Holly Creek system is a separate region of high diversity that emerged as a secondary priority. The Mill Creek sub-watershed of Tennessee and the Sumac Creek sub-watersheds are also ranked moderately high because they are upstream of species-rich sections of the mainstem. From a conservation ecology perspective, it makes sense to pursue a management strategy focused on two separate population areas: 1. the mainstem and headwaters, which provide habitat for most of the listed species and 2. Holly Creek, which provides habitat for about half of the invertebrate species as well as *Cyprinella caerulea* (blue shiner), *Etheostoma trisella* (trispot darter), and *Percina kusha* (bridled darter). Notably, the headwaters of both of these systems are already partially protected in National Forests and any future preservation efforts can build on this base.

Modeling suggested that the lower Coahulla Creek could be favorable habitat for several species, although only *P. lenticula* has been recorded there in recent years. It is possible that additional species once inhabited this small river but were extirpated by past land use activities and channel modifications. Historic agriculture has been implicated in the loss of other fish species in the Southeast (Harding et al., 1998; Maloney et al., 2008; Wenger et al., 2008), but the degree of impact in the Conasauga remains a matter of speculation. Alternatively, it is possible that we omitted important environmental variables that describe natural differences between the Coahulla system and other parts of the Conasauga sub-basin. In any case, the Coahulla is not ranked as a high priority, and the fact that few imperiled species are currently present mean that it is not a candidate for preservation, although future restoration activities should perhaps not be ruled out.

One question is the degree to which middle tributaries of the Conasauga should be targeted for preservation and restoration. Sugar Creek, Sumac Creek, and Georgia's Mill Creek (Murray County) rank only moderately high and yet are upstream of important habitat in the mainstem. We suggest that management efforts in these sub-watersheds be focused on identifying and mitigating any obvious stressors, rather than large-scale land preservation and restoration. It is perhaps most important that agricultural producers in this region use appropriate best management practices to minimize nutrient and pesticide transport downstream, which have been identified as two likely stressors contributing to declines in some mainstem mussel species (Sharpe and Nichols, 2007).

A limitation of our approach is the simplistic upstream-downstream loss response function we employed, which assumes that upstream watersheds are important for protecting downstream watersheds, but that the reverse does not hold true. The complex life histories of mussel species (Strayer et al., 2004) implies the need for connectivity for dispersal and *E. trisella* and *E. ditrema* are known to make short spawning migrations (Boschung and Mayden, 2004), which means that connectivity between downstream feeding habitat and upstream spawning habitat can be important. Quantifying the degree of dependence of upstream sub-watersheds on their downstream neighbors is not straightforward, however. In contrast, because likely stressors in the system are transported downstream (Sharpe and Nichols, 2007), we considered it essential that there be some dependence of downstream sub-watersheds on their upstream neighbors. However, this is a simple first approximation that should be revisited in the future with a more thorough, species-by-species consideration of the importance of connectivity.

Linke et al., (2007), building on others (Margules and Pressey, 2000; Sarkar et al., 2006), suggested that watershed conservation planning should consider three key attributes: irreplaceability, condition, and vulnerability. "Irreplaceability" is the probability that the sub-watershed is essential to meeting conservation goals. Our use of the Zonation algorithm was intended to rank the sub-watersheds of the Conasauga from irreplaceable (or most critical) to irrelevant to the purpose of conserving imperiled aquatic species. "Condition" considers whether the sub-watershed is degraded or of high quality. The most highly ranked sub-watersheds in our analysis are of generally good condition and are candidates for preservation, while lower ranked sub-watersheds tend to be degraded and may be candidates for restoration. However, condition can vary greatly within sub-watersheds and within highly ranked sub-watersheds there may be individual sites that are degraded and which would also be strong candidates for restoration. "Vulnerability" is the likelihood that the sub-watershed will be exposed to land use changes that will degrade its condition. We did not incorporate this into our prioritization scheme, although we suggest that it be a consideration in site-level decision making. Among two otherwise equally valuable parcels, one that is subject to change in the near future may be more of a priority than one that is considered unlikely to change.

We suggest that a prioritization such as the one conducted here should be a mandatory step in any watershed supporting species of conservation interest prior to the initiation of any significant program of preservation or restoration. Such an exercise should also be repeated periodically as conditions change and new data are collected. With the free availability of user-friendly tools such as the MaxEnt and Zonation software, these analytical methods can be employed by any governmental agency or non-governmental organizations with a conservation focus. While prioritizations such as this are not without their limitations and caveats, we think that conservation efforts would benefit from their more general application.

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TABLE 1. Federally and state protected fish species of the Conasauga River sub-basin.

Genus species	Common Name	State status	Federal status
Cyprinella caerulea	blue shiner	E	T
Macrhybopsis sp. cf. *aestivalis*	Coosa chub	E	-
Noturus sp. cf. *munitus*	Coosa madtom	E	-
Etheostoma sp. cf. *brevirostrum*	holiday darter	E	-
Etheostoma ditrema	coldwater darter	E	-
Etheostoma trisella	trispot darter	E	-
Percina antesella	amber darter	E	E
Percina jenkinsi	Conasauga logperch	E	E
Percina kusha	bridled darter	E	-
Percina lenticula	freckled darter	E	-

TABLE 2. Federally and state protected invertebrate species of the Conasauga River sub-basin.

Genus species	Common Name	State status	Federal status
Cambarus cymatilis	Conasauga blue burrower	E	-
Elliptio arca	Alabama spike	E	-
Elliptio arctata	delicate spike	E	-
Hamiota altilis	finelined pocketbook	T	T
Medionidus acutissimus	Alabama moccasinshell	T	T
Medionidus parvulus	Coosa moccasinshell	E	E
Pleurobema decisum	southern clubshell	E	E
Pleurobema georgianum	southern pigtoe	E	E
Pleurobema hanleyianum	Georgia pigtoe	E	-
Ptychobranchus greenii	triangular kidneyshell	E	E
Strophitus connasaugensis	Alabama creekmussel	E	-
Strophitus subvexus	southern creekmussel	E	-

TABLE 3. Relative contribution of environmental predictor variables for each modeled species. “Records” indicates the number of unique sites with a positive species occurrence used in the analysis for each species. The numbers in the remaining columns indicate the percent contribution of that predictor variable to the predictive model for each species.

Species	Records	Area	Dams	Elevation	TIA	Forest
blue shiner	218	91.7	4.3	2.6	1.2	0.2
speckled chub	26	92.7	4.1	2.7	0.3	0.2
holiday darter	21	68.6	7.6	10.0	9.4	4.3
trispot darter	93	88.2	5.3	5.5	0	0.9
amber darter	31	94.2	5.2	0.6	0	0
Conasauga logperch	32	93.9	2.6	2.2	0.3	1.1
bridled darter	30	77.6	7.9	8.7	2.6	3.2
Alabama spike	16	95.5	0.5	0.9	3.0	0.1
finelined pocketbook	155	90.8	5.4	1.8	0.8	1.2
southern clubshell	49	98.3	0	0.6	1.1	0
southern pigtoe	34	92.1	3.1	0.7	3.9	0.1
Georgia pigtoe	15	95.8	1.9	1.0	1.1	0.3
triangular kidneyshell	27	94.6	0.9	1.6	2.9	0
Alabama creekmussel	55	89.8	7.9	1.1	0.7	0.6

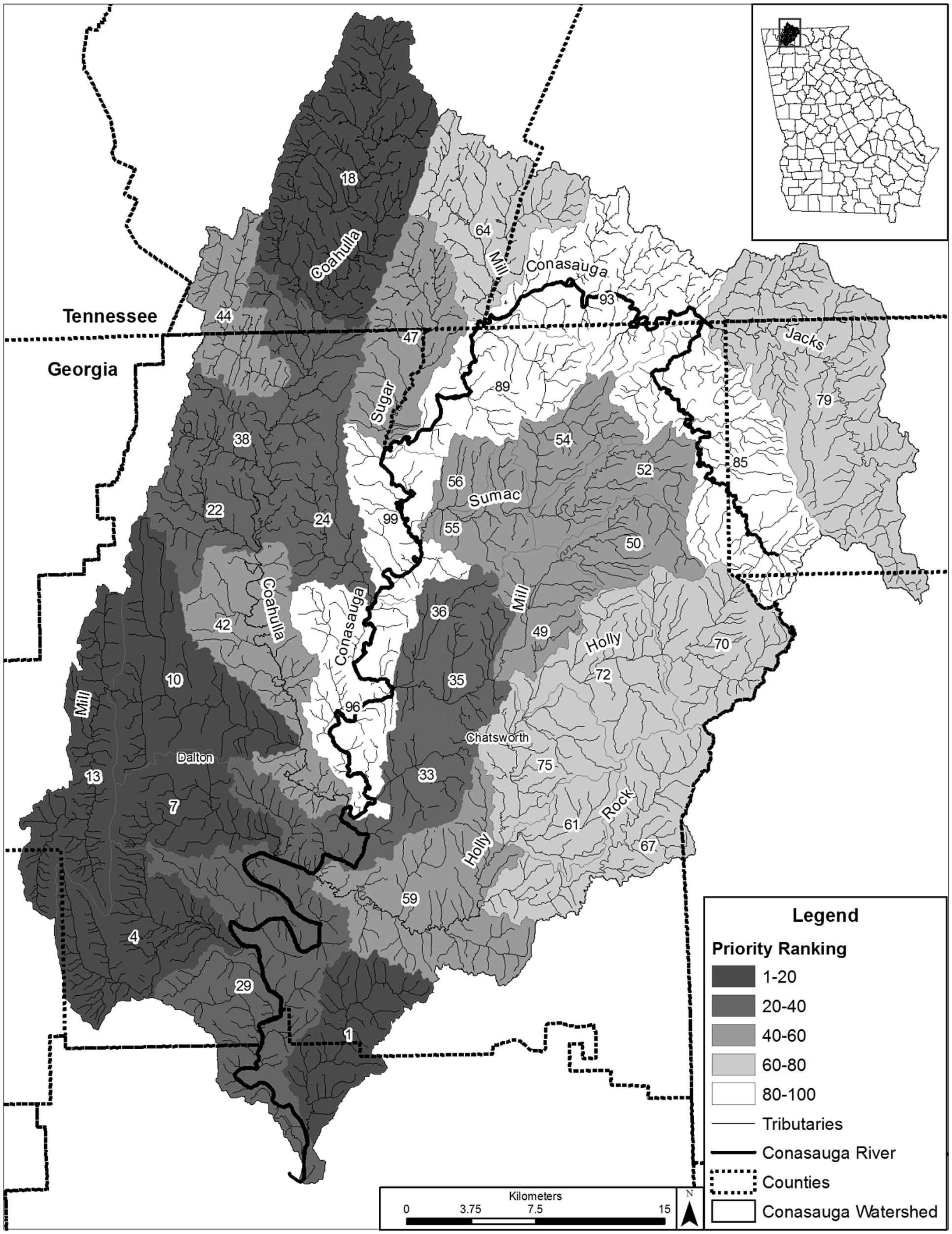

FIGURE 1. Prioritization of Conasauga HUC-12 sub-watersheds. Priority values on a scale of 1-100 are shown on the map for each sub-watershed.